MOLECULAR SYSTEMATICS, EVOLUTION, AND POPULATION BIOLOGY IN THE MUSTARD FAMILY (BRASSICACEAE)[1]

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ABSTRACT

The present review summarizes results from the past decade on the systematics, population genetics, and evolutionary biology of the mustard family, Brassicaceae (Cruciferae). The research of various authors is discussed and presented in the context of ongoing and accumulating studies. The review is useful in view of the immensely increasing work on *Arabidopsis thaliana*, the model species of plant molecular biology, and on important crop plants such as species of *Brassica*. Traditional and molecular-based phylogenies are critically discussed, new generic alignments are proposed, and groups in need of molecular studies are identified. Unfortunately, knowledge obtained from molecular genetics and development of *A. thaliana* is only very slowly creeping into the systematics of Brassicaceae. Future directions of research should move beyond assessing generic relationships or limits, and should also address character development and evolution, the molecular basis of various homoplastic characters, the nature of the genome, and many other new challenges that are emerging from detailed molecular studies of *A. thaliana*.

Key words: *Arabidopsis*, Brassicaceae, Cruciferae, evolution, literature review, molecular systematics, polyploidy, population biology, speciation.

The Brassicaceae are an important family for three primary reasons. First, the family includes several crop plants grown worldwide, some of which have been cultivated since prehistoric times. Various species are grown for oil, mustard condiments, forage and fodder for animals, or as vegetables (Crisp, 1976; Simmonds, 1986). The most important members belong to the genus *Brassica* L., including varieties of *B. oleracea* L. (broccoli, brussels sprouts, cabbage, cauliflower, kale, kohlrabi, savoy), *B. juncea* (L.) Czern. (Indian mustard), *B. nigra* (L.) W. D. J. Koch (black mustard), *B. napus* L. var. *napobrassica* (L.) Rchb. (rutabaga), *B. napus* var. *napus* (rape), and *B. rapa* L. (summer turnip rape, Chinese mustard, Chinese cabbage). Other locally important crops are *Lepidium sativum* L. (cress), *L. meyenii* Walp. (maca), *Armoracia rusticana* P. Gaertn., B. Mey. & Scherb. (horseradish), *Raphanus sativus* L. (radish), *Sinapis alba* L. and *B. juncea* (both used in the manufacture of table mustard), *Nasturtium officinale* R. Br. (watercress), *Cochlearia officinalis* L. and *Cardamine amara* L. (bittercress), *Eruca vesicaria* (L.) Cavan. var. *sativa* (Mill.) Thell. (rucola or erugula), and *Eutrema wasabi* (Siebold) Maxim. (wasabi). Second, many species of the genera *Aethionema* R. Br., *Alyssum* L., *Arabis* L., *Aubrieta* Adans., *Draba* L., *Erysimum* L., *Hesperis* L., *Iberis* L., *Lobularia* Desv., *Lunaria* L., and *Matthiola* R. Br. are cultivated as ornamentals (Al-Shehbaz, 1984). Third, *Arabidopsis thaliana* (L.) Heynh. (thale cress) is considered to be the most important flowering plant for conducting experimental work in various fields of biology, including plant genetics, physiology, development, pathology, genetic engineering, and related fields. In recent years, *A. thaliana* has become a model system for plant molecular biology, which has culminated in the recent publication of its complete genomic sequence (The Arabidopsis Genome Initiative, 2000), also available via the World Wide Web (⟨http://www.nature.com/genomics/papers/a_thaliana.html⟩). *Arabidopsis thaliana* has a small genome, is fast growing, easy to cultivate with minimal space and care demands, and self-pollinating

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with a high fecundity (Meyerowitz, 1989; Patrusky, 1991). Moreover, genetic modifications by transformation are routinely accomplished to generate mutants or to over-express particular genes. Stock centers distribute seeds of different accessions and mutants, mapping populations, DNA libraries, YACs (yeast artificial chromosomes), and BACs (bacterial artificial chromosomes) for molecular analysis in genetics and development. A central question for this research program is how to apply knowledge gained from the model system (i.e., laboratory lines/strains of *A. thaliana*) to wild plant species. A wealth of information on *A. thaliana* is being assembled electronically (⟨http://www.aspb.org/publications/arabidopsis⟩), and it should be consulted by biologists from all fields.

In order to understand the evolutionary processes and interactions of plants with their environment, it is necessary to work with wild species and populations. Representatives of the mustard family show remarkable variability in certain characters. Important variable traits include resistance to insects and fungi, tolerance to heavy metals and salt, apomixis, annual versus perennial life cycles, and morphological characters such as leaf architecture, fruit diversity, development of woody tissue, seed production, and trichome morphology. Therefore, an increasing number of molecular and evolutionary biologists are focusing on the study of the wild relatives of *A. thaliana* (e.g., Pennisi, 2000a, 2000b; Nasrallah et al., 2000).

As traditionally delimited, the Brassicaceae include about 340 genera and some 3350 species distributed worldwide, especially in temperate regions of the Northern Hemisphere (Al-Shehbaz, 1984; Appel & Al-Shehbaz, 2002). The family, which has long been recognized as a natural group, is well defined morphologically and has a fairly uniform flower structure. The flowers are radially symmetrical and consist of four almost always free sepals in two whorls, four free petals (though sometimes lacking), often six, free, tetradynamous stamens (outer 2 shorter than inner 4; though many species of the large genus *Lepidium* L. have four or only two stamens), and a bicarpellate ovary almost always with a false septum (a partition dividing the ovary into two locules). On the other hand, fruits of Brassicaceae exhibit enormous diversity in size, shape, and structure. They are the source of the most important diagnostic characters for the delimitation and identification of taxa at various ranks. The fruits are often dehiscent, 2-valved capsules divided longitudinally by a septum, though in many genera the fruits are indehiscent and/or the septum is totally lacking. Some groups are characterized by angustiseptate fruits (compressed at a right angle to the septum), such as the members of tribe Lepidieae sensu Schulz (1936), while in the majority of the family the fruits are either latiseptate (compressed parallel to the septum) or not flattened (terete or angled in cross section). On the basis of length/width ratio, the fruits have been traditionally divided into silicles (length less than three times width) or siliques (length more than three times width), but such division, though useful for identification, is arbitrary and has limited phylogenetic utility (Al-Shehbaz, 1984; Appel & Al-Shehbaz, 2002). Additional important taxonomic characters include embryologic features (position of cotyledons in relation to radicle), nectar-gland morphology, trichome types, growth forms, chromosome number, and seed-coat anatomy and surface.

Several classification systems were proposed from the early 19th to the mid 20th century, the most notable of which are those of de Candolle (1821), Prantl (1891), Hayek (1911), Schulz (1936), and Janchen (1942). According to these systems, the Brassicaceae can be divided into anywhere from 4 to 19 tribes and 20 to 30 subtribes. Recent molecular studies (e.g., Koch et al., 2001a) suggest that these taxonomic subdivisions mostly do not reflect phylogenetic relationships. Molecular data strongly support a sister relationship between Cleomoideae (Capparaceae) and Brassicaceae (Rodman et al., 1994). On the basis of a little generic sampling, Judd et al. (1994) proposed merging Brassicaceae and Capparaceae in one family, but recent molecular data (J. C. Hall et al., 2002) clearly support the maintenance of Brassicaceae, Capparaceae, and Cleomaceae as three distinct but closely related families.

A better understanding of evolution within Brassicaceae can be achieved only by a comprehensive review of studies ranging from the population level to analyses from the infraspecific level to the entire family. This should take into account data from anatomy, morphology, chorology, cytology, population biology, ecology, and molecular systematics, including results from studies of *A. thaliana*. The present paper summarizes several important aspects of evolution within Brassicaceae and reviews relevant literature from the past decade on molecular marker systems used to reach a better understanding of phylogeny, evolutionary trends, and patterns of variation at the population level and above. The review specifically identifies new challenges in the systematics and phylogeny of Brassicaceae, proposes a few generic alignments and groupings, and determines groups most in need of studies.

1. Speciation Processes: Polyploidy and Hybridization

The origin of polyploids and the mechanisms behind the establishment of newly evolved populations and taxa are among the many challenging questions in plant sciences (Ramsey & Schemske, 1998; Thompson & Lumaret, 1992; Petit et al., 1999; Soltis & Soltis, 1993, 1999). Recent studies of the overall genome structure of hybrid and polyploid taxa provide new insights about the dynamic nature of complete genomes. The data obtained in these studies were generated on the basis of artificial hybrids or by comparative mapping (Rieseberg et al., 1999; Rieseberg & Linder, 1999; Lagercrantz, 1998; Kowalski et al., 1994; Axelsson et al., 2000). Comparative genome analysis of some Brassicaceae (Acarkan et al., 2000) has shown that structural rearrangements occurred with a significantly higher frequency in polyploid *Brassica* than in diploid *Arabidopsis thaliana* or *Capsella rubella* Reut. By contrast, Axelsson et al. (2000) have shown that the genome of *B. juncea* remained almost unchanged since the species originated as an allopolyploid hybrid between *B. nigra* and *B. rapa*. Unfortunately, such studies are based only on a few cultivated species of *Brassica* and on *A. thaliana*, and hardly anything is known about other polyploids in the family, especially those with very high chromosome numbers such as *Cardamine diphylla* (Michx.) A. Wood ($2n = 256$), which has the highest known number in Brassicaceae (see Al-Shehbaz, 1984). Polyploidy is widespread in the Brassicaceae, occurring in at least 37% of the species (Appel & Al-Shehbaz, 2002); some genera (e.g., *Crambe* L., *Moricandia* DC., *Vella* L.) appear to be exclusively polyploid (Al-Shehbaz, 1984). If we consider the diploid species of *Brassica* and other genera (e.g., *Physaria* (Nutt. ex Torr. & A. Gray) A. Gray, including *Lesquerella* S. Watson) as "palaeopolyploids" (see below), the percentage of polyploid taxa in the family will be at least 50% (authors' compilation). Allopolyploidy is probably the most common mode of hybrid speciation in the Brassicaceae and accounts for the majority of polyploid species (authors' compilation). However, phylogenetic studies are needed to determine if speciation in polyploids occurred at rates higher than in diploids.

Molecular methods have helped to elucidate the complex evolutionary history of many allopolyploid groups in the family. *Arabidopsis suecica* (Fr.) Norrl. ($n = 13$), an allopolyploid species derived from *A. thaliana* ($n = 5$) and *A. arenosa* (L.) Lawlrée ($n = 8$) (Mummenhoff & Hurka, 1994, 1995; Kamm et al., 1995; O'Kane et al., 1997; Comai et al., 2000), is one of the best studied species of hybrid origin. Other studies include *Brassica* (Palmer et al., 1983; Erickson et al., 1983; Lagercantz & Lydiate, 1996), *Arabis holboellii* Hornem. (Sharbel & Mitchell-Olds, 2001; Koch et al., 2003a), *Capsella* Medik. (Mummenhoff & Hurka, 1990; Hurka & Neuffer, 1997), *Cardamine* ×*insueta* Urbanska and *C. schulzii* Urbanska (Urbanska et al., 1997; Franzke & Mummenhoff, 1999), *Cardamine* ×*enriquei* Marhold et al. (Marhold et al., 2002b), *Diplotaxis* DC. (Mummenhoff et al., 1993), *Draba* (Brochmann et al., 1992a, 1992b, 1992c; Widmer & Baltisberger, 1999a), *Nasturtium* R. Br. (Bleeker et al., 1999), and *Rorippa* Scop. (Bleeker & Hurka, 2001). More recently, research focusing on hybridization and polyploidization among cruciferous plants has been attributed additional importance because of the successful crosses between the model organism *Arabidopsis thaliana* and its wild relative *A. lyrata* (L.) O'Kane & Al-Shehbaz subsp. *petraea* (L.) O'Kane & Al-Shehbaz ($n = 8$) (see Nasrallah et al., 2000).

A knowledge of the patterns of speciation and species relationships within a group of plants is critical for the understanding of its morphological evolution. *Lepidium*, which exhibits more floral diversity than any other genus of Brassicaceae, shows that more than half of its species lack the lateral stamens and most of these also have reduced petals. The species with reduced flowers are distributed primarily in the Americas and Australia/New Zealand. Previous phylogenetic studies with noncoding regions of cpDNA and rDNA ITS showed incongruences in most New World species relationships (Bowman et al., 1999; Mummenhoff et al., 2001a). This, combined with the presence of many polyploid species, implied a reticulate history of the genus, but did not provide enough information to infer the evolutionary pattern of flower structures. To address this question more thoroughly, sequences of the first intron of a single copy nuclear gene, *PISTILLATA* (*PI*), were determined from 43 *Lepidium* species. The phylogenetic analysis of the *PI* intron suggests that many species in the New World might have originated from allopolyploidization correlated with floral reduction. Interspecific hybrids were generated to test this hypothesis, and the phenotypes of F_1 flowers indicate allelic dominance of the absence of lateral stamens. This suggests that propagation of dominant alleles through interspecific hybridization could account for the abundance of the allopolyploid species without lateral stamens (Lee et al., 2002).

Hybridization and reticulation have been exten-

sively analyzed at the molecular level on the North American *Arabis* ×*divaricarpa* A. Nels. focusing on concerted evolution of the internal transcribed spacer regions 1 and 2 (Koch et al., 2003b). In this case study it is remarkable that apomixis also played an important role in speciation and differentiation.

Polyploidy also played an important role in the evolution of species complexes, particularly during time periods greatly influenced by glaciation and deglaciation. This holds true for *Arabidopsis suecica* in Scandinavia (Mummenhoff & Hurka, 1994, 1995; O'Kane et al., 1997), the *Cardamine pratensis* complex (Franzke & Hurka, 2000), *Cardamine amara* (Marhold et al., 2002a), and *Cochlearia* L. in Europe (Koch et al., 1996, 1998a; Koch, 2002). Furthermore, diversification of most species of *Draba* (Koch & Al-Shehbaz, 2002; Brochmann et al., 1992a, 1992b) is best interpreted by reticulation and polyploidization during the last few million years. In the absence of significant glacial influence, however, hybridization, reticulation, and polyploidy apparently have played an important role in the evolution of old species complexes in the genera *Yinshania* Ma & Y. Z. Zhao in China (Koch & Al-Shehbaz, 2000) and *Microthlaspi* F. K. Mey. in the Balkans (Koch et al., 1998c; Koch & Hurka, 1999).

We now have the molecular tools to unravel the origin of (alloploid) hybrid taxa. But techniques such as genome mapping and QTL analysis will allow us to study many details of hybridization and speciation (Bradshaw et al., 1995; Rieseberg et al., 1995). It is also important to measure in future studies the relative fitness of hybrids and parental taxa in a range of habitats to further elucidate the role of natural hybridization (Arnold, 1997). Furthermore, to test the evolutionary importance of hybridization in a given species complex, it is critical that findings from greenhouse/population cage experiments be tested in the field (Arnold et al., 2001).

2. Populational Differentiation, Phenotypic Plasticity, and Adaptation

In order to elucidate speciation processes and phylogenetic relationships between species, it is necessary to understand intra-population dynamics and genetics. Numerous phenotypic traits have been analyzed in Brassicaceae, including local adaptation across climatic gradients in *Arabis fecunda* Rollins (McKay et al., 2001) and *Capsella* (Hurka, 1990; Hurka & Neuffer, 1997; Neuffer & Hurka, 1999; Neuffer & Hoffrogge, 1999), survivorship in *Arabis laevigata* (Muhl. ex Willd.) Poir. (Bloom et al., 2001), glucosinolate accumulation during plant/insect interaction in *Arabidopsis thaliana* (Kliebenstein et al., 2001), and herbivore resistance and pollination in *Brassica rapa* (Strauss et al., 1999). *Capsella bursa-pastoris* (L.) Medik. was studied for maternal effects upon germination behavior (Neuffer & Koch, 1996), mechanical stress (Neuffer & Meyer-Walf, 1996), flowering time (Neuffer & Hurka, 1986; Neuffer & Bartelheim, 1989; Neuffer, 1990), and leaf morphology (Neuffer, 1989). Detailed analysis of host-pathogen interaction and their coevolution have been analyzed in Brassicaceae (Constantinescu & Fatehi, 2002), particularly in *Arabis* (Roy, 2001), and studies have focused on phenotypic plasticity, reaction norm, and its evolution in *A. thaliana* (Pigliucci & Byrd, 1998; Pigliucci & Schmitt, 1999; Pigliucci et al., 1999; Pigliucci & Marlow, 2001; Pigliucci, 2002; Pollard et al., 2001). Many of these investigations have also used molecular markers, isozymes, or RAPDs to study intra- and interpopulational differentiation (see Appendix 1, parts II and III).

The majority of these investigations have, however, neglected the genetic diversity stored in the soil seed bank. Depending on the type of seed bank and the reproductive biology of the selected species, the seed bank may play an essential role in the recruitment and establishment of new generations. The spatial genetic structure of the subpopulations (surface and aboveground populations) represented by seeds may account for significant changes in the genetic constitution of plant populations during their history. The soil seed bank not only reduces the rate of genetic erosion (e.g., via genetic drift), but also may compensate environmental changes in space and time. Of the seven known studies focusing on seed-bank genetics (Tonsor et al., 1993; Alvarez-Buylla & Garay, 1994; McCue & Holtsford, 1998; Mahy et al., 1999; Cabin, 1996; Evans et al., 2000; Koch et al., 2003a), the last three were conducted on members of the Brassicaceae.

3. Convergent Evolution of Morphological Characters: Molecular Phylogenetic Studies Contradict Traditional Systems of Tribal Classification

Traditionally, the Brassicaceae have been divided into tribes and subtribes on the basis of relatively few characters (morphology, embryology). Major disagreements are readily observed by comparison of the systems of Hayek (1911), Schulz (1936), and Janchen (1942). Molecular data dem-

onstrate that morphological variation used traditionally in these three classification systems does not provide phylogenetically informative characters to distinguish several groups (Koch et al., 2001a). The major drawback of all the classification systems proposed thus far is their almost complete failure to accommodate convergence of morphological characters. In fact, molecular studies reveal homoplasy in almost every conceivable morphological character in the Brassicaceae (Price et al., 1994; Zunk et al., 1996; Mummenhoff et al., 1997a; Koch & Mummenhoff, 2001; Mummenhoff et al., 2001a, 2001b). For example, gamosepaly, which is rare in the family, has recently been shown to have evolved independently in at least 12 genera (Al-Shehbaz, 2001). As for fruit morphology and cotyledon position in relation to the radicle, which are extensively used in every facet of taxonomy in the family, convergence is so widespread that extreme care should be taken in classification and delimitation of taxa solely based on these characters. A classic example is demonstrated by the genera *Arabis* and *Arabidopsis* Heynh., both of which are characterized by linear and narrow fruits, branched trichomes, and cotyledons that are primarily accumbent. Recent molecular studies (Koch et al., 1999a, 2000, 2001a; Al-Shehbaz & O'Kane, 2002a; O'Kane & Al-Shehbaz, in prep.) have provided ample evidence that both genera are polyphyletic, and an overemphasis on these homoplastic characters is the main reason for their artificial delimitation. Conversely, taxa that appear to be quite different morphologically may in fact be very closely related. For example, *Draba* exhibits enormous morphological diversity in habit, trichome type, flower color, chromosome number, and fruit morphology, but molecular data clearly support its monophyly (Koch & Al-Shehbaz, 2002). For *Thlaspi* L., molecular data (Mummenhoff & Koch, 1994; Zunk et al., 1996; Mummenhoff et al., 1997a, 1997b; Koch & Mummenhoff, 2001) provide strong support for the recognition of several segregates as proposed by Meyer (1973, 1979) based on seed-coat anatomy. The molecular phylogeny of *Thlaspi* is not congruent with the traditional classification of Schulz (1936) based on fruit form. Several lineages in the molecular tree include *Thlaspi* species with diverse fruit types, whereas species with the same fruit type belong to different clades, thus providing strong evidence for convergence in fruit traits. As for *Lepidium*, the cpDNA sequence phylogeny once again demonstrates the widely artificial nature of the traditional classification schemes, and it shows that fruit morphology (e.g., thickening, compression, and union of valves) is not a reliable phylogenetic marker in this genus (Brüggemann, 2000; Mummenhoff et al., 2001a). Numerous other examples of homoplasy in almost every conceivable morphological character can be demonstrated in *Cochlearia* L. (Koch et al., 1999b; Koch & Al-Shehbaz, 2000), *Arabis* and *Arabidopsis* (Koch et al., 1999a), *Draba* (Koch & Al-Shehbaz, 2002), *Cardamine* L. (including *Dentaria* L.: Franzke et al., 1998; Sweeney & Price, 2000), *Microthlaspi* (Koch & Mummenhoff, 2001), and the halimolobine clade (Bailey et al., 2002).

Some traditionally recognized tribes have been shown to be polyphyletic, including Arabideae and Lepidieae (Koch et al., 1999a, 2000, 2001a) and Sisymbrieae (Koch et al., 2001a; Bailey et al., 2002). Moreover, boundaries between the tribes Lepidieae, Lunarieae, Sisymbrieae, Euclidieae, and Alysseae are highly artificial (Zunk et al., 1993; Price et al., 1994). The tribes Brassiceae, Thelypodieae, and Lepidieae have long been thought to be natural groups (Al-Shehbaz, 1973, 1984; Zunk et al., 1999), but the results of Koch et al. (2001a) strongly suggest that the Lepidieae are polyphyletic. This tribe is based solely on the presence of angustiseptate fruits (Schulz, 1936), a feature that in fact evolved independently within Lepidieae, Brassiceae (e.g., *Psychine* Desf., *Schouwia* DC.), and Thelypodieae (*Caulanthus californicus* (S. Watson) Payson). Moreover, *Capsella*, *Lepidium*, and *Thlaspi* s.l., which have been placed in Lepidieae in every system of classification of the family, are clearly unrelated, and *Capsella* shows more affinities to *Arabidopsis* than to either *Lepidium* or *Thlaspi* (Koch et al., 2001a; O'Kane & Al-Shehbaz, in prep.).

Monophyly of the Brassiceae is shown in a series of studies summarized in Warwick and Black (1997a, 1997b). Members of this tribe are characterized by having segmented (heteroarthrocarpous) fruits and/or conduplicate cotyledons (Appel & Al-Shehbaz, 2002), and there is strong evidence that reversals in one or both characters have taken place. Segmented fruits and conduplicate cotyledons are among a few characters in the family where convergent evolution apparently has not occurred.

The Heliophileae, a tribe comprising six South African genera that mostly have diplecolobal cotyledons (Appel & Al-Shehbaz, 1997), are also likely monophyletic. Preliminary ITS sequence data (Mummenhoff et al., unpublished) strongly support the monophyly of *Heliophila* L. and related genera. However, the phylogenetic relationships within Heliophileae are unresolved, and the smaller genera *Brachycarpaea* DC., *Cycloptychis* E. Mey. ex Sond., *Schlechteria* Bolus, *Silicularia* Compton, and *Thlas-*

peocarpa C. A. Sm. are all well nested within *Heliophila* and might not be taxonomically distinct from it. The last genus exhibits far more diversity in habit, leaf morphology, flowers, fruits, and seeds than any other genus in Brassicaceae.

Outside of the Brassiceae and Heliophileae, the cotyledonary position is unreliable in tribal delimitation. Within several genera (e.g., *Erysimum*) or even species (e.g., *Lepidium virginicum* L.) one finds both accumbent and incumbent cotyledons, the most common types in the family. In summary, it appears that except for these two tribes, the remainder of the family is not readily divided into large monophyletic groups based solely on single morphological characters. Critical re-examinations of morphology, anatomy, and palynology, in the light of molecular phylogenies, are needed to subdivide the family into monophyletic groups based on character combinations rather than individual characters. Such studies have already identified some monophyletic clades, including the polycolpate, cardaminine, and halimolobine clades (see below).

4. Advances in Molecular Systematics

Critical phylogenetic relationships within the tribe Brassiceae have identified six reasonably well-defined groups corresponding to subtribes. However, traditional taxonomy (e.g., Gómez-Campo, 1999; Gómez-Campo & Prakash, 1999) did not take into consideration the overwhelming molecular data that have accumulated over the past decade, and *Brassica*, *Diplotaxis*, *Erucastrum*, and *Sinapis* continue to be artificially delimited following Schulz (1936). The characters separating these genera (e.g., seeds uniseriate vs. biseriate, valves 1-veined vs. more than 1-veined, racemes bracteate vs. ebracteate) exhibit enormous homoplasy throughout the family, yet they are taken in these genera as reliable characters. According to molecular data (Warwick & Black, 1997b), species of all four genera fall into two monophyletic groups, the nigra and rapa clades, that also include many smaller or monotypic genera. In our opinion, taxa within the rapa and nigra clades need extensive studies to establish monophyletic groups and to redefine generic boundaries based on critical re-evaluation of morphology. Warwick and Black (1997a) also clearly demonstrated that *Cakile* Mill., *Didesmus* Desv., and *Erucaria* Gaertn. form an unresolved clade. *Cakile* is distinguished primarily by having corky (instead of non-corky) fruits and obsolete (vs. distinct) styles. Corky fruits evolved independently in some species of *Crambe* and *Raphanus*, and this feature is unreliable for generic delimitation, as is the style length. Although all three genera were maintained by Appel and Al-Shehbaz (2002), further studies may prove that they are congeneric.

Molecular data (Warwick & Black, 1994; Crespo et al., 2000) provided ample evidence that *Boleum* Desv. and *Euzomodendron* Coss. are nested within *Vella*, which prompted Warwick and Al-Shehbaz (1998) and Appel and Al-Shehbaz (2002) to recognize one genus, *Vella*. Of the entire Brassiceae, these are the only three genera with united inner staminal filaments and a base chromosome number of $x = 17$. However, Gómez-Campo (1999: 19) maintained all three because they "exhibit very distinct sets of adaptive characters . . . for seed dispersal." These "adaptive characters" (presence of distinct vs. vestigial seed wing, seed number, fruit dehiscence) are also homoplastic elsewhere in the family and, therefore, should not be overemphasized at the expense of the extensive molecular data now available. In fact, fruit indehiscence evolved independently numerous times not only within Brassiceae but in the entire family (Appel & Al-Shehbaz, 2002; Mummenhoff et al., 2001a). Of the 337 genera of Brassicaceae recognized by Appel and Al-Shehbaz (2002), 125 are monotypic and about an additional 100 contain two to four species (oligotypic). Molecular studies show that several of the monotypic genera are indistinguishable from other larger genera. For example, both *Agallis* Phil. and *Twisselmannia* Al-Shehbaz are nested within and should be united with *Tropidocarpum* Hook., whereas *Hugueninia* Rchb. should be united with *Descurainia* Webb & Berthel. (Price & Al-Shehbaz, 2003). Other examples include the union of *Lycocarpus* O. E. Schulz with *Sisymbrium* and *Neobeckia* Greene with *Rorippa* (Price, pers. comm.), *Boleum* and *Euzomodendron* with *Vella* (Warwick & Black, 1994; Crespo et al., 2000), *Iti* Garn.-Jones & P. N. Johnson with *Cardamine* (Mitchell & Heenan, 2002), *Pachyphragma* (DC.) Rchb. and *Gagria* M. Král with *Thlaspi* s. str. (Mummenhoff et al., 2001b), and *Drabopsis* K. Koch with *Draba* (Al-Shehbaz & Koch, in prep.). We believe that upon a combination of molecular studies and critical evaluation of morphology the vast majority of monotypic or oligotypic genera will eventually be merged with other genera.

Molecular data indicate that the largest genera of the family, including *Draba* (350 spp.), *Lepidium* (ca. 220 spp.), *Cardamine* (200 spp.), *Erysimum* (180 spp.), and *Physaria* and *Lesquerella* combined (100 spp.), are monophyletic. Studies are needed to demonstrate monophyly of *Alyssum* (170–190 spp.), including *Meniocus* Desv. and *Ptilotrichum* C.

A. Mey., and *Rorippa* Scop. (75 spp.). *Erysimum* is taxonomically one of the most difficult genera of the family, and it is much in need of extensive phylogenetic studies. Phylogenetic studies on *Sisymbrium* (Warwick et al., 2002) show that the genus is polyphyletic, that it should consist of 43 Old World and 1 New World species, and that the remaining 46 species in the New World belong to other genera allied to the Thelypodieae sensu Al-Shehbaz (1973).

As for *Arabis*, molecular studies (Koch et al., 1999a, 2000; O'Kane & Al-Shehbaz, in prep.; Price, pers. comm.) clearly demonstrate that it is polyphyletic and that most of the species recognized by Rollins (1993) should be assigned to *Boechera* A. Löve & D. Löve, *Turritis* L., *Pennellia* Nieuwl., and *Arabidopsis*, whereas some of the European species (sensu Jones & Akeroyd, 1993) should be assigned to *Fourraea* Greuter & Burdet and *Arabidopsis*. *Arabis* has been traditionally delimited solely by having branched trichomes, flat and linear fruits, and accumbent cotyledons, a combination of characters found in many other genera of Brassicaceae. The entire *Arabis* complex is much in need of further morphological and molecular studies, but all of these segregates do not appear to be closely related to the core of *Arabis* that includes the type species, *A. alpina* L.

Extensive studies on *Lepidium* (Brüggemann, 2000; Mummenhoff, 1995; Mummenhoff & Hurka, 1991; Mummenhoff et al., 1992, 1995, 2001a; Zunk et al., 1999) have clearly demonstrated the genus should include *Cardaria* Desv., *Coronopus* Zinn, and *Stroganowia* Kar. & Kir. and that the last two genera are polyphyletic. Based on such data and on a critical re-evaluation of morphology, Al-Shehbaz et al. (2002) united all three with *Lepidium*. Although *Lepidium* shows more diversity in the reductions of petals and stamens than any other genus in the family (Bowman & Smyth, 1998; Bowman et al., 1999), it is well defined by having angustiseptate (rarely terete or 4-angled) fruits and two subapical ovules one in each locule. Other genera that show this combination of characters (e.g., *Acanthocardamum* Thell., *Delpinophytum* Speg., *Stubendorffia* Schrenk ex Fisch., C. A. Mey. & Avé-Lall., *Winklera* Regel) should also be studied, and it is quite possible that they, too, might be congeneric with *Lepidium*.

The polycolpate clade (Al-Shehbaz & O'Kane, 2002b; O'Kane & Al-Shehbaz, 2002) is a monophyletic New World group readily distinguished from the remaining 96% of Brassicaceae by having 4–10-colpate instead of strictly 3-colpate pollen. The clade comprises *Physaria* (including *Lesquerella*), *Dimorphocarpa* Rollins, *Dithyrea* Harv., *Lyrocarpa* Hook. & Harv., *Nerisyrenia* Greene, *Paysonia* O'Kane & Al-Shehbaz, and *Synthlipsis* A. Gray. Sequence data of this group (O'Kane & Al-Shehbaz, unpublished) in GenBank have recently been taken by Kropf (2002) in his comprehensive ITS tree. The results support the monophyly of the *Physaria* clade and place it between *Arabidopsis* and *Olimarabidopsis* Al-Shehbaz et al.

Although no comprehensive study has been conducted on the cardaminine clade, a compilation of various works (Bleeker et al., 2002a, 2002b; Franzke et al., 1998; Les, 1994; Mitchell & Heenan, 2000; Sweeney & Price, 2000; Price & Sweeney, pers. comm.) shows that it consists of *Cardamine* (including *Dentaria* and *Iti*), *Nasturtium*, *Rorippa* (including *Neobeckia*), *Barbarea* R. Br., *Armoracia*, *Iodanthus* (Torr. & A. Gray) Steud., *Leavenworthia* Torr., *Planodes* Greene, and *Selenia* Nutt. The vast majority of taxa in this clade occupy wet or mesic habitats, are glabrous or rarely have simple trichomes, and have dissected or compound leaves, elongated fruits, and mostly accumbent cotyledons. A few exceptions occur, but this is a well-defined group that perhaps includes the genera *Lignariella* Baehni, *Neomartinella* Pilger, *Ornithocarpa* Rose, *Pegaeophyton* Hayek & Hand.-Mazz., *Raphanoryncha* Rollins, *Subularia* L., *Taphrospermum* C. A. Mey., and *Yinshania*. The analysis of Kropf (2002) appears to be erroneous because it shows *Rorippa* nested within *Cardamine* and *Iti* (New Zealand) forming a sister group with the unrelated *Bivonaea* DC. (Mediterranean) instead of being nested within *Cardamine* (Mitchell & Heenan, 2000).

The halimolobine clade is an exclusively New World group that consists of *Halimolobos* Tausch, *Mancoa* Wedd., *Pennellia* Niewl., *Sphaerocardamum* Schaur, and, yet to be described, a new segregate genus (Bailey et al., 2002). Almost all members of this clade have dendritic trichomes, plump seeds, incumbent cotyledons, entire or dentate leaves, and small white flowers with subtetradynamous stamens. The clade is related to other North American genera with branched trichomes, including *Boechera*, *Cusickiella* Rollins, and *Beringia* Price et al., but some South American species of *Sisymbrium* that have dendritic trichomes, all excluded from the genus (Warwick et al., 2002), should also be tested.

A morphologically well-defined group of primarily central Asian genera (e.g., *Chartoloma* Bunge, *Glastaria* Boiss., *Goldbachia* DC., *Isatis* L., *Litwinowia* Woronow, *Pachypterygium* Bunge, *Pugionium* Gaertn., *Sameraria* Desv., *Schimpera* Hochst.

& Steud., *Spirorhynchus* Kar. & Kir., *Tauscheria* Fisch. ex DC.) has not been studied phylogenetically, and it probably forms a monophyletic clade. All members are characterized by having indehiscent, 1- or 2-seeded, primarily angustiseptate fruits, yellow or rarely whitish flowers, sessile often auriculate cauline leaves, and simple or no trichomes (Appel & Al-Shehbaz, 2002). Only ITS data for *Isatis* are available, and the genus appears to be related to those with angustiseptate fruits and simple or no trichomes (Kropf, 2002).

Based on ITS data (Warwick et al., 2002), most of the New World American genera with simple or no trichomes, as well as *Pringlea* (six islands in the South Indian Ocean), form a large unresolved clade that includes members of the Thelypodieae sensu Al-Shehbaz (1973). This clade encompasses taxa with enormous fruit diversity, and extensive molecular and morphological studies are needed to resolve its generic limits. Among the genera that fall in this clade are most of the South American *Sisymbrium*, *Dryopetalum* A. Gray, *Hesperidanthus* (B. L. Rob.) Rydb., *Mostacillastrum* O. E. Schulz, *Sibara* Greene, and *Werdermannia* O. E. Schulz. Other genera that should be studied are *Chilocardamum* O. E. Schulz, *Dictyophragmus* O. E. Schulz, *Eremodraba* O. E. Schulz, *Neuontobotrys* O. E. Schulz, *Phlebiophragmus* O. E. Schulz, *Phlebolobium* O. E. Schulz, *Polypsecadium* O. E. Schulz, and *Sarcodraba* Gilg & Muschl. Pepper and Norwood (2001) have shown *Caulanthus* S. Watson to be polyphyletic and, together with *Guillenia* Greene, is nested within *Streptanthus* Nutt. In our opinion, these three genera, plus *Streptanthella* Rydb. and *Sibaropsis* S. Boyd & T. S. Ross, are perfectly at home in the more inclusive *Streptanthus*.

Trichome type is a feature used extensively in the delimitation of genera of Brassicaceae. Branched trichomes apparently evolved independently at least two or three times in the family (Galloway et al., 1998; Koch et al., 2001a; Kropf, 2002). However, little is known about the genetic background behind the shift in trichome morphology. Knowledge of the molecular basis of trichome development in *Arabidopsis thaliana* (see the excellent review of Szymanski et al., 2000) is rapidly expanding. Once the genes coding for the development of various trichomes are identified and sequenced, we should be able to use these markers as potentially powerful tools in phylogenetic studies in the family. Such knowledge will also help in understanding the origin of glabrous from the pubescent state, or vice versa.

Similarly, fruit type in the family is also essential in generic delimitation. Once the developmental and molecular bases of various fruit and seed characters (e.g., segmented vs. unsegmented fruits, corky vs. non-corky ones, dehiscent vs. indehiscent, seeded vs. seedless segments, winged vs. wingless seeds, flattened vs. terete valves) are understood, the taxonomy of the family could be based on more solid foundations. The differences in fruit characters often are overemphasized at the expense of more useful features that are largely ignored. Two examples demonstrate that. First, *Twisselmannia* was shown by Price and Al-Shehbaz (2003) to be identical to *Tropidocarpum* in their chloroplast gene *ndh*F and nuclear ITS. *Twisselmannia* has short (4–5 mm long), obtriangular, 4- to 8-seeded fruits superficially resembling those of *Capsella bursa-pastoris*, whereas *Tropidocarpum* has longer (10–70 mm) narrowly linear or oblong, 16–70-seeded fruits. These genera are indistinguishable in every aspect of habit, leaf, raceme, flower, and seed morphology. Second, based on nuclear and chloroplast DNA sequences, Mummenhoff et al. (2001b) have clearly demonstrated that *Alliaria* (with linear, wingless, subterete to 4-angled fruits) is nested within *Thlaspi* s. str. (obcordate, winged, strongly angustiseptate fruits). Traditional taxonomy (e.g., Schulz, 1936) places *Alliaria* in the tribe Sisymbrieae and *Thlaspi* in the Lepidieae. Both genera have concentrically striate seeds, a character not known elsewhere in the Brassicaceae, and molecular data strongly indicate that they should be united, a position with which we agree. In this context, it is important to note that fruit dehiscence (also a diagnostic character for generic delimitation; see above) and the relative length of fruit are controlled in *A. thaliana* by only few MADS-box genes, i.e., *SHATTERPROOF* and *FRUITFULL* (Liljegren et al., 2000; Ferrandiz et al., 2000). We conclude that fruit characters alone may well lead to erroneous taxonomic conclusions, and that such characters should be critically evaluated in light of molecular and other morphological data.

Arabidopsis represents a classic example where molecular studies have contributed to a better understanding of its taxonomy and generic delimitation. The approximately 60 binomials previously assigned to the genus are now placed in 14 genera (Al-Shehbaz et al., 1999) and, as presently circumscribed (O'Kane & Al-Shehbaz, 1997; Al-Shehbaz & O'Kane, 2002a), *Arabidopsis* includes only nine species. Support for the new segregate genera proposed by Al-Shehbaz et al. (1999) comes from ITS sequences (Koch et al., 1999a; O'Kane & Al-Shehbaz, 2002, and in prep.), chalcone synthase (Koch et al., 2001a), *mat*K (Koch et al., 2001a), and alcohol dehydrogenase (Miyashita et al., 1998).

Perhaps the most surprising finding from molecular data is the basal position of the genus *Aethionema* R. Br. in relation to the rest of Brassicaceae (Zunk et al., 1993, 1996, 1999; Galloway et al., 1998; Koch et al., 2001a). Although only the highly variable *A. grandiflorum* Boiss. & Hohen. ($n = 14$) has been studied, the basal position of the genus poses several challenging questions. First, *Aethionema*, which is a highly polymorphic genus of 50–60 species (primarily Turkey and the Middle East), is much in need of detailed systematic and phylogenetic studies (Appel & Al-Shehbaz, 2002). Second, fruit morphology in the genus (angustiseptate, 2- to 8-seeded) has traditionally been considered as specialized (Schulz, 1936). Third, *Aethionema* exhibits enormous diversity in chromosome numbers ($n = 7, 8, 11, 12, 14, 16, 18, 21, 22, 24, 30$; see Appel & Al-Shehbaz, 2002). Without critical phylogenetic studies of *Aethionema* and several other southwestern Asian genera, it is premature to speculate as to what an ancestral mustard might look like. It is interesting to note that members of the Thelypodieae (New World) were considered at one point as primitive (Al-Shehbaz, 1973) but now are treated as relatively specialized (Galloway et al., 1998).

Although substantial molecular data have accumulated during the past ten years, only data on ITS sequences are somewhat more extensive than those of other markers. Such data are being synthesized by Bailey et al. (pers. comm.), and it is premature to make any generalizations. The compilation by Kropf (2002) of largely unpublished sequences from GenBank is far from adequate. It would be rewarding to assemble similar large data sets on chloroplast genes and compare them with those of ITS sequences. Most studies have concentrated on North American and European taxa, and except for the work of Mitchell and Heenan (2000) and Hurka et al. (unpublished) on the mustards of New Zealand and Australia, respectively, hardly any studies exist on the South American, African, Himalayan, and central Asian genera of the family. Molecular studies on disjunctions, especially in cosmopolitan genera such as *Cardamine*, *Lepidium*, and *Rorippa*, which occur on all continents except Antarctica, are needed, though the works of Mummenhoff et al. (2001a), Lee et al. (2002), and Mummenhoff et al. (in prep.) on *Lepidium* are ideal studies to follow.

The vast majority of molecular studies in Brassicaceae involved sequences of single markers, but it is far more important to study multiple markers separately and combined, as was done by Bailey et al. (2002) and Koch et al. (2001a). Now that the entire genome of *Arabidopsis* is well known and the function of many of its genes has been identified, it is highly desirable that phylogenetic studies be based on sequences of genes with definite functions, especially those controlling the development of trichomes, leaves, and fruits, structures that offer the taxonomic characters most frequently used. Equally important is to determine on the basis of molecular data the evolution of individual characters and the distribution of their homoplasy on a family-wide basis. For example, we have no idea if the presence of multicellular multiseriate glands represents a synapomorphy within the family, and the evolution of many other characters (e.g., schizocarpic or samaroid fruits, palmately compound leaves, decurrent stigmas with united lobes, stellate trichomes with webbing and numerous rays, segmented fruits, conduplicate or diplecolobal cotyledons, production of garlic smell, to name a few) needs critical studies. A good example illustrating this aspect is the determination of evolutionary changes in leaf development (Bharathan et al., 2002) and floral structure in *Lepidium* (Bowman et al., 1999; Lee et al., 2002) and fruit convergence in *Thlaspi* (Mummenhoff et al., 1997a), but studies such as these are needed on many other characters. The absence of a given feature in *Arabidopsis thaliana* should also stimulate research to trace if this species still has at least part of the genome responsible for that character. The studies of self-incompatibility in *Brassica* and its homolog in *Arabidopsis* (Conner et al., 1998; Kusba et al., 2001) are excellent examples to follow.

5. *Arabidopsis* and Its Wild Relatives: Genome Synteny and Comparative Molecular Approaches

Molecular markers are widely used to study the organization of plant genomes, and genetic-linkage maps based on molecular markers have been assembled for many plant species (Schmidt, 2000). The use of identical sets of markers can lead to the construction of comparative genetic maps of species. Such experiments give an idea about the degree of conservation of gene repertoire and structure of markers among different species. Additional information about genome regions between markers can be obtained by cloning and characterizing these regions using information from the flanking regions. If there are high levels of genome co-linearity, as well as of the gene level (microsynteny), comparative genome-mapping experiments can serve as an efficient tool for transferring information and resources from well-studied genomes, such as that of *Arabidopsis*, to related plants. Sequencing

the entire genome of *Arabidopsis thaliana* (The Arabidopsis Genome Initiative, 2000; Blanc et al., 2000; Vision et al., 2000; Simillion et al., 2002) have shown that at least 70% of the genome is duplicated and that the original haploid number of its ancestors was probably four, doubled to eight, and reduced to five as a result of extensive chromosomal rearrangements, fusion, and loss.

Brassica has been thoroughly studied using comparative mapping experiments (Lagercrantz & Lydiate, 1996; Kowalski et al., 1994; Lagercrantz, 1998). Other studies (Kowalski et al., 1994; Lagercrantz, 1998; Grant et al., 1998; Lagercrantz et al., 1996; Cavell et al., 1998; Jackson et al., 2000; O'Neill & Bancroft, 2000; Axelsson et al., 2001; Quiros et al., 2001) have focused on the *Arabidopsis–Brassica* comparison. These results have substantiated the view that "diploid" species of *Brassica*, *B. nigra* ($n = 8$), *B. oleracea* ($n = 9$), *B. rapa* ($n = 10$), have largely triplicated genomes and most likely have descended from a polyploid ancestor. Comparative mapping experiments have demonstrated that approximately 90 rearrangements occurred since the divergence of *Arabidopsis* and *B. nigra*, estimated to have occurred 14–20 million years ago (Koch et al., 2000, 2001a; Vision et al., 2000). Higher degrees of genome co-linearity have been observed in comparisons between *A. thaliana* and *A. lyrata* subsp. *petraea* (diverged ~5 MYA; De Haen et al., 1999) and *A. thaliana* and *Capsella rubella* (diverged ~6.2 to 9.8 MYA; Schmidt et al., 2001; Acarkan et al., 2000). Co-linearity on a small scale (microsynteny) has been detected in several regions in *Arabidopsis* and *Brassica* (Sadowski et al., 1996; Sadowski & Quiros, 1998; Conner et al., 1998; Osborn et al., 1997), although no general conclusions can be drawn from these studies. However, similar homologous segments with drastically increased fragment sizes were found. Nevertheless, genome co-linearity is extensive enough to permit the application in *Brassica* species of a lot of information assembled in the framework of the *Arabidopsis* genome project. For the first time, a combinatorial approach of analyzing microsynteny (based on DNA sequence information) and function (gene expression analysis) has been performed on a large set of cruciferous plants using promoter regions of APETALA3, and CHS (Koch et al., 2001b). This analysis among distantly related species may help to predict gene and promoter functions and specificity, and may also help achieve a deeper understanding of the evolutionary significance and consequences of mutations in coding regions (Stotz et al., 2000; Bishop et al., 2000). Comparative genome studies are essential for understanding genome co-linearity, duplications, deletions, and rearrangements, as well as for determining the evolution of duplicated genomes through time and the unification of genomes within polyploids (A. E. Hall et al., 2002). In our opinion, more studies of this kind, though both labor intensive and rather costly, are needed, especially for understanding the evolution of major clades of Brassicaceae and the role polyploidy played during their evolution.

6. Migration and Phylogeography

Molecular markers have been utilized as a tool to assess geographic distribution patterns in groups whose diversification has not substantially been influenced by the environment. Maternally inherited DNA markers (e.g., the plastome of most angiosperms; see Harris & Ingram, 1991; Reboud & Zeyl, 1994) can be used to trace the maternal lineages. A variety of nuclear markers are used in such studies: either "co-dominant" such as isozymes and microsatellites, or dominant such as "RAPDs" (random amplified polymorphic DNAs) or "AFLPs" (amplified fragment length polymorphisms), as well as DNA sequences of nuclear regions such as the frequently used internal transcribed spacers of nuclear ribosomal DNA (ITS-1 and ITS-2) (Franzke et al., 1998; Francisco-Ortega et al., 1999; Bleeker et al., 2002b). These nuclear markers serve as tools to detect patterns of genetic diversity that are inherited maternally and paternally. By using molecular markers, biogeographical (source areas of genetic diversity, vicariant patterns, migration routes, hybridization zones, secondary contact zones, etc.) and related evolutionary questions (speciation processes, polytopic origin, etc.) can be addressed, and the data obtained serve to develop more appropriate models that explain present-day distribution and diversity. A recent example for such analyses is the coordinated effort to develop a deeper understanding of distribution patterns, group differentiation, and the evolution of plants in the arctic and alpine regions (Stehlik et al., 2001). Both *Biscutella* L. (Dannemann, 2000; Tremetsberger et al., 2002) and *Cochlearia* (Koch, 2002) include some species of alpine plants that have been subjected to such studies. Other studies on European *Arabis alpina* L. (Plantholt, 1995), *Cardamine* (Franzke & Hurka, 2000), and Eurasian *Microthlaspi* (Koch et al., 1998c; Koch & Hurka, 1999) helped to elucidate colonization routes from refugial areas into formerly glaciated areas of northern and central Europe. The analyses of *Arabidopsis thaliana* have demonstrated distribution patterns of

genetic diversity that are congruent with those found in other plant and animal species, all of which demonstrate that the Iberian Peninsula, Italy, and the Balkans represented three major refugial areas during glaciation in central Europe (Sharbel et al., 2000). A complex speciation and migration scenario in *Draba* was elaborated for North, Central, and South America (Koch & Al-Shehbaz, 2002). *Draba* also shows strong affinities to high alpine regions (e.g., in the Alps, Scandinavia, the Himalayas, Rocky Mts., Andes) and, therefore, its evolution appears to have been influenced by glaciation and deglaciation periods throughout the Pleistocene. Studies on the Chinese *Yinshania* elucidated migration over long distances and extensive reticulation during migration (Koch & Al-Shehbaz, 2000). It is remarkable that, in all cases analyzed to date, polyploidization played an important role in migration and phylogeography, and this seems also to be the case in *Lepidium*. Comprehensive molecular studies of the biogeographic history of *Lepidium* and *Rorippa* on a worldwide scale were conducted by Mummenhoff et al. (2001a) and Bleeker et al. (2002a), respectively. The easily dispersible mucilaginous seeds of species of *Lepidium* and the widespread occurrence of autogamous breeding systems suggest a rapid radiation of the genus by long-distance dispersal during the Pliocene/Pleistocene, an interpretation supported by estimates of divergence times based on cpDNA sequence divergence. Climatic changes resulted in the establishment of arid/semiarid areas, thus providing favorable conditions for the radiation of *Lepidium* that led to its current worldwide distribution.

Lepidium is represented in Australia and New Zealand by 19 and 7 native species, respectively. ITS and cpDNA phylogenies gave strongly conflicting signals and provided evidence for bicontinental hybrid genomic constitution in *Lepidium* in these areas (Mummenhoff et al., submitted). Seventeen Australian/New Zealand species share a Californian cpDNA type. As for ITS, nine species appear to harbor a Californian type and eight species share a South African type. This pattern is most likely explained by two trans-oceanic dispersals of *Lepidium* from California and Africa into Australia/New Zealand and subsequent hybridization followed by homogenization of the ribosomal DNA either to the Californian or South African ITS type in the two different lineages.

Some future directions of research should focus on the origin and early diversification of Brassicaceae. There are two contradicting hypotheses: a western North American and Irano-Turanian origin (Hauser & Crovello, 1982). Molecular and morphological studies at the family level are needed to understand the early evolutionary history and dispersal of Brassicaceae. Other research directions should focus on the range extension of species, as recent global climatic changes and human activities will lead to the spread of species beyond their natural ranges or the reduction of their ranges (Walther et al., 2002). Studies on *Arabidopsis* and *Teesdalia* R. Br. demonstrate the influence of climate on the global ranges of species (Hoffmann, 2000, 2002). Such studies may provide information about the ecogeographic amplitude of species. Species of some genera (e.g., *Nasturtium*, *Cardamine*) have been cited as examples where hybridization may serve as a stimulus for the evolution of invasiveness (Ellstrand & Schierenbeck, 2000).

7. Molecular Clock Estimates from DNA Sequence Variation and the Age of Brassicaceae

The reliability of molecular clock estimates of evolutionary divergence has been the subject of much debate (Sanderson, 1998; Soltis & Soltis, 2001). Questions largely involve: (1) the possibility of varying substitution rates within a lineage, (2) differing substitution rates between lineages, and (3) the lack of accurate evidence to calibrate the molecular clock (e.g., missing fossil evidence) (Sanderson, 1998, 2002; Britton et al., 2002; Syvanen, 2002). Estimates from *Chs* (chalcone synthase), *Adh* (alcohol dehydrogenase), and *mat*K (maturase K) indicate that the Brassicaceae appeared approximately 50 million years ago (MYA) (Koch et al., 2001a). Synonymous substitution rates of 1.5×10^{-8} at *Chs* and *Adh*, and 1.7×10^{-9} at *mat*K were estimated (Koch et al., 2000, 2001a). Substitution rates obtained from these studies were used to calculate that *Arabidopsis thaliana* diverged from its *Cardaminopsis*-like common ancestor approximately 5 MYA, while the most recent common ancestor of polymorphic *A. thaliana* accessions occurred roughly 1.5 MYA (the average divergence time between *Brassica* and *Arabidopsis* has been calculated to be 14–20 MYA; Koch et al., 2000). These results correspond to findings obtained from divergence time estimates of the mitochondrial gene for NADH subunit 4 (*nad*4) in *Brassica* species by Yang et al. (1999b). These data also help to calibrate other molecular clocks of more widely used markers in Brassicaceae, such as the ITS or *trn*L intron and *trn*L-F spacer region (Mummenhoff et al., 2001a; Bleeker et al., 2002b). Despite the inherent uncertainties associated with rate and time estimates outlined by Sanderson (1998), this procedure has been

found to be useful in many studies of plant evolution and biogeography (Böhle et al., 1996; Kim et al., 1998; Vargas et al., 1998). Meanwhile, an approach to estimate divergence times in the absence of rate constancy has been developed (Sanderson, 1997). As for Brassicaceae, it would be desirable to calibrate substitution rates of widely used nuclear, cpDNA, and mtDNA marker systems by reference to alternative/more substantiated fossil records, geological history/events, and palaeoclimatic data (Baldwin & Sanderson, 1998; Richardson et al., 2001).

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Appendix 1. Molecular Markers in the Study of Systematics and Evolution of Brassicaceae: A Literature Survey

The following list summarizes studies in which various methods have been used to study the evolution and systematics of Brassicaceae. The compiled literature is sorted according to the marker systems used, listed alphabetically by taxa and then by authors. The list is restricted to studies at the populational level or above.

I. Isoelectric focusing of ribulose-1,5-bisphosphate carboxylase (IEF-Rubisco):

Arabidopsis including *Cardaminopsis* (C. A. Mey.) Hayek (Mummenhoff & Hurka, 1994).
Capsella bursa-pastoris (Mummenhoff & Hurka, 1990).
Diplotaxis (Mummenhoff et al., 1993).
Erysimum (Mummenhoff & Jentzsch, 1994).
Lepidium (Mummenhoff, 1989, 1995; Mummenhoff & Hurka, 1991; Mummenhoff et al., 1992).
Thlaspi (Koch et al., 1993; Mummenhoff & Zunk, 1991).

II. Isozyme analysis:

Arabidopsis including *Cardaminopsis* (Mummenhoff & Hurka, 1995).
A. lyrata subsp. *petraea*, as *Arabis petraea* L. (Schierup, 1998).
Arabis (Roy & Rieseberg, 1989).
A. fecunda (McKay et al., 2001).
A. serrata Franch. & Sav. (Oyama et al., 1993).
Biscutella (Tremetsberger et al., 2003).
Boechera A. & D. Löve, as *Arabis* (Roy, 1995; Roy & Rieseberg, 1989).
Brassica (Chevre et al., 1995; Simonsen & Heneen, 1995a, 1995b).
B. insularis Moris (Petit et al., 2001).
Brassicaceae (Chevre et al., 1995).
Brassiceae (Anderson & Warwick, 1999; Simonsen & Heneen, 1995a, 1995b).
Capsella (Hurka, 1990; Hurka & Düring, 1994; Hurka & Neuffer, 1997; Neuffer & Hurka, 1999).
C. bursa-pastoris (Neuffer, 1996; Neuffer & Hoffrogge, 1999; Neuffer & Hurka, 1999; Neuffer et al., 1999).
C. rubella (Neuffer & Hoffrogge, 1999).
Cardamine (Urbanska et al., 1997).
C. amara (Koch et al., 2003a; Marhold et al., 2002a).
C. pratensis L. agg. (Franzke & Hurka, 2000).
Cochlearia (Koch et al., 1998a; Koch, 2002).
Draba (Brochmann, 1992; Brochmann et al., 1991, 1992a, 1992b, 1992c; Scheen et al., 2002).
Lesquerella fendleri (A. Gray) S. Watson (Cabin, 1996).
Microthlaspi (Koch & Hurka, 1999).
Nasturtium (Bleeker et al., 1999).
Raphanus sativus (Huh & Ohnishi, 2001).
Rorippa (Bleeker & Hurka, 2001).
Streptanthus Nutt. (Mayer et al., 1994).
Thlaspi caerulescens J. & C. Presl (Koch et al., 1998b).
Warea carteri Small (Evans et al., 2000).

III. Restriction fragment length polymorphism of
(a) chloroplast (cp) DNA:
Arabidopsis, including *Cardaminopsis* (Mummenhoff & Hurka, 1995; Price et al., 1994).
Arabideae (Price et al., 1994).
Brassica (Song et al., 1995; Warwick & Black, 1991, 1993, 1994, 1997a, 1997b; Warwick et al., 1992).
Brassicinae (Warwick & Black, 1991, 1993, 1994, 1997a, 1997b).
Brassiceae (Pradhan et al., 1992; Warwick & Black, 1994, 1997a).
Cakilinae (Warwick & Black, 1997a).
Cardamine (Urbanska et al., 1997).
Diplotaxis (Warwick et al., 1992).
Draba (Brochmann et al., 1992c).
Lepidieae (Zunk et al., 1993; Zunk et al., 1999).
Lepidium (Mummenhoff et al., 1995).
Microthlaspi (Koch et al., 1998c).
Moricandiineae (Warwick & Black, 1994).
Raphaninae (Warwick & Black, 1997a).
Savignyinae (Warwick & Black, 1994).
Sisymbrieae (Price et al., 1994).
Streptanthus (Mayer & Soltis, 1994).
Thelypodieae (Zunk et al., 1996).
Thlaspidineae (Zunk et al., 1996).
Thlaspi (Mummenhoff & Koch, 1994; Mummenhoff et al., 1997a, 1997b; Zunk et al., 1996).
Vellinae (Warwick & Black, 1994).
Zillinae (Warwick & Black, 1994).
(b) nuclear ribosomal DNA:
Brassica (Delseny et al., 1990; Maluszynska & Heslop-Harrison, 1993; Waters & Schaal, 1996).
Eruca Mill. (Lakshmikumaran & Negi, 1994).
Microthlaspi (Koch et al., 1998c).
(c) total nuclear DNA:
Brassica (Song et al., 1995).
(d) mitochondrial DNA:
Brassica (Song et al., 1995).

IV. Random amplified polymorphic DNA (RAPD):
Capsella bursa-pastoris (Neuffer, 1996; Neuffer et al., 1999; Yang et al., 1998).
Cardamine (Neuffer & Jahncke, 1997; Urbanska et al., 1997).
C. amara (Lihová et al., 2000).
C. pratensis agg. (Franzke & Hurka, 2000).
Cochlearia (Koch et al., 1996).
Draba (Scheen et al., 2002).
Lepidium meyenii (Toledo et al., 1998).

V. Amplified fragment length polymorphism (AFLP):
Arabidopsis thaliana (Sharbel et al., 2000).
Cardamine amara (Marhold et al., 2002b).
Cheesemania O. E. Schulz, *Pachycladon* Hook. f. (Mitchell & Heenan, 2002).

VI. repetitive DNA and microsatellites:
Alliaria petiolata (M. Bieb.) Cavara & Grande (Meekins et al., 2001).
Arabidopsis, including *Cardaminopsis* (Kamm et al., 1995; Van der Zwan et al., 2000).
A. lyrata subsp. *petraea* (van Treuren et al., 1997).
Brassica (Harrison & Heslop-Harrison, 1995; Saal et al., 2001).
Diplotaxis (Martin & Sanchez-Yelamo, 2000).

VII. DNA Sequencing of
(a) coding plastid genes:
maturase K:
Brassicaceae (Koch et al., 2001a).
***ndh*F:**
Cardamine, including *Dentaria* (Les, 1994; Sweeney & Price, 2000).
***rbc*L:**
Arabidopsis (Price et al., 1994; Tsukaya et al., 1997).
Capparales (Rodman et al., 1993, 1996).
Armoracia, *Nasturtium*, *Neobeckia*, *Rorippa* Les (1994).
(b) non-coding plastid *trn*L intron and spacer:
Arabis (Roy, 2001).
A. holboellii (Sharbel & Mitchell-Olds, 2001).
Boechera (Roy, 2001).
Brassica (Lannér, 1998).
Cardamine, including *Dentaria* (Franzke et al., 1998; Sweeney & Price, 2000; Bleeker et al., 2002b).
C. pratensis agg. (Franzke & Hurka, 2000).
Caulanthus S. Watson, including *Guillenia* Greene (Pepper & Norwood, 2001).
Cochlearia (Koch et al., 1999b).
Draba (Koch & Al-Shehbaz, 2002).
Halimolobos Tausch (Bailey et al., 2002).
Lepidium (Mummenhoff et al., 2001a).
Mancoa Wedd. (Bailey et al., 2002).
Pennellia Nieuwl. (Bailey et al., 2002).
Rorippa (Bleeker & Hurka, 2001; Bleeker et al., 2002a).
Sphaerocardamum Schauer (Bailey & Doyle, 1999; Bailey et al., 2002).
Streptanthus (Pepper & Norwood, 2001).
Yinshania (Koch & Al-Shehbaz, 2000).
(c) nuclear coding alcohol dehydrogenase (ADH):
Arabidopsis (Miyashita et al., 1996, 1998).
A. thaliana (Hanfstingl et al., 1994; Innan et al., 1996).
Arabis (Miyashita et al., 1996, 1998).

Brassicaceae (Koch et al., 2000).
Leavenworthia Torr. (Charlesworth et al., 1998).
(d) nuclear coding S-alleles:
Arabidopsis lyrata (Charlesworth et al., 2000).
A. thaliana (Charlesworth et al., 2000).
Brassica (Charlesworth et al., 2000; Uyenoyama, 2000).
(e) nuclear coding chalcone synthase (CHS):
Brassicaceae (Koch et al., 2000, 2001a).
(f) nuclear coding arginine decarboxylase (ADC):
Brassicaceae (Galloway et al., 1998).
(g) nuclear coding 2S albumin:
Arabidopsis, *Brassica* (Boutilier et al., 1999).
(h) nuclear coding myrosinase:
Arabidopsis, *Brassica* (Rask et al., 2000).
(i) nuclear coding acidic chitinase:
Arabidopsis thaliana (Kawabe et al., 1997).
Arabis (Bishop et al., 2000).
(j) nuclear coding chalcone isomerase:
Arabidopsis, including *Cardaminopsis* (Kuittinen & Aguade, 2000).
(k) nuclear coding floral homeotic genes (APETALA, PISTILLATA, CAULIFLOWER):
Arabidopsis thaliana (Lowman & Purugganan, 1999; Purugganan & Suddith, 1998, 1999).
Brassica (Lowman & Purugganan, 1999; Purugganan et al., 2000).
(l) nuclear non-coding internal transcribed spacer of ribosomal DNA (ITS):
Arabidopsis (O'Kane et al., 1997; Yang et al., 1999a).
Arabis (Koch et al., 1999a; Roy, 2001).
Boechera (Roy, 2001; Koch et al., 2003b).
Brassica (Yang et al., 1999a, 1999b; Warwick et al., 2002).
Brassicaceae (Heenan et al., 2002; Mitchell & Heenan, 2000).
Cardamine, including *Dentaria* (Franzke & Mummenhoff, 1999; Franzke et al., 1998; Bleeker et al., 2002b).
C. pratensis agg. (Franzke & Hurka, 2000).
Caulanthus, including *Guillenia* (Pepper & Norwood, 2001; Warwick et al., 2002).
Cochlearia (Koch et al., 1999b).
Crambe (Francisco-Ortega et al., 1999).
Descurainia Webb & Berthel. (Bricker et al., 2000).
Draba (Beilstein & Windham, 2002; Koch & Al-Shehbaz, 2002; Widmer & Baltisberger, 1999a, 1999b).
Dryopetalum A. Gray (Warwick et al., 2002).
Erucastrum C. Presl (Warwick et al., 2002).
Halimolobos (Bailey et al., 2002).
Hornungia (Kropf, 2002).
Hymenolobus (Kropf, 2002).
Lepidium (Bowman et al., 1999).
Mancoa (Bailey et al., 2002).
Mostacillastrum O. E. Schulz (Warwick et al., 2002).
Neotorularia Hedge & J. Léonard (Warwick et al., 2002).
Pachyphragma (DC.) Rchb. (Mummenhoff et al., 2001b).
Pennellia (Bailey et al., 2002).
Pringlea W. Anderson ex Hook. f. (Warwick et al., 2002).
Pritzelago (Kropf, 2002).
Romanschulzia O. E. Schulz (Warwick et al., 2002).
Rorippa (Yang et al., 1999a; Bleeker et al., 2002b).
Schoenocrambe Greene (Warwick et al., 2002).
Sibara Greene (Warwick et al., 2002).
Sisymbrium (Warwick et al., 2002).
Sphaerocardamum (Bailey & Doyle, 1999; Bailey et al., 2002).
Stanleya Nutt. (Warwick et al., 2002).
Streptanthella Rydb. (Warwick et al., 2002).
Streptanthus (Pepper & Norwood, 2001; Warwick et al., 2002).
Thelypodiopsis Rydb. (Warwick et al., 2002).
Thelypodium Endl. (Warwick et al., 2002).
Thlaspi (Koch & Mummenhoff, 2001; Mummenhoff et al., 1997a, 1997b, 2001b).
Vellinae (Crespo et al., 2000).
Warea Nutt. (Warwick et al., 2002).
Yinshania (Koch & Al-Shehbaz, 2000).
(m) chalcone synthase promoter region:
Brassicaceae (Koch et al., 2001b).
(n) alcohol dehydrogenase promoter region:
Arabidopsis halleri (L.) O'Kane & Al-Shehbaz subsp. *gemmifera* (Matsum.) O'Kane & Al-Shehbaz (Miyashita, 2001).
A. thaliana (Miyashita, 2001).
(o) *apetala*3 promoter region:
Brassicaceae (Koch et al., 2001b).
(p) pistillata-intron:
Halimolobos (Bailey et al., 2002).
Mancoa (Bailey et al., 2002).
Pennellia (Bailey et al., 2002).
Sphaerocardamum (Bailey & Doyle, 1999; Bailey et al., 2002).
Lepidium (Lee et al., 2002).
(q) coding mitochondrial *nad*4:
Arabidopsis (Yang et al., 1999a).
Brassica (Yang et al., 1999a, 1999b).
VIII. Comparative mapping approaches, segregation analysis:
Arabidopsis (Acarkan et al., 2000; Vision et al., 2000).
Brassica or *Brassica-Arabidopsis* (Axelsson et al., 2000, 2001; Bohuon et al., 1996; Cavell et al., 1998; Conner et al., 1998; Lagercrantz, 1998; Lagercrantz et al., 1996; Lan & Paterson, 2000, 2001; Lan et al., 2000; Rossberg et al., 2001; Ryder et al., 2001; Schmidt, 2000; Schmidt et al., 2001; Sillito et al., 2000).
Capsella bursa-pastoris (Linde et al., 2001).
Capsella rubella (Acarkan et al., 2000; Rossberg et al., 2001).
Review (Schmidt, 2000; Schmidt et al., 2001).
IX. Short interspersed elements (SINE):
Brassiceae (Lenoir et al., 1997).